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EFFECTS OF WATER STRESS ON PHOTOSYNTHESIS AND RESPIRATION OF TWO POPULATIONS OF SWEETGUM

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EFFECTS OF WATER STRESS ON PHOTOSYNTHESIS AND RESPIRATION OF TWO POPULATIONS OF SWEETGUM

INTRODUCTION

Sweetgum (Liquidambar styraciflua L.) is an important tree throughout its native range both for commercial and ornamental use and it has been widely planted elsewhere as a shade tree. The botanical range of sweetgum extends along the Coastal Plain and Piedmont from Connecticut to eastern Texas, with the exception of southern Florida. It grows in the Mississippi and Ohio Valleys as far north as southern Illinois, Indiana and Ohio. It occurs also in the mountains of Mexico and Central America (Martindale, 1958).

Throughout its range in the United States, sweetgum attains its best growth and is most important as a part of the vegetation on moist bottomland sites, although it will grow on dryer uplands (Chittenden, 1906; Oosting, 1942; Thomas, 1961). In the northern part of its range, it seems to be more strictly limited to the lower, wetter sites (Trenk, 1929; Stearns, 1957), but it grows at altitudes over 2000 ft. in the Southern Appalachian Mountains. Sweetgum survives on severely eroded old fields where pines do not. Its seedlings are somewhat tolerant

of inundation (Hosner, 1958). Work with seedlings (Wenger, 1952; Ferrell, 1953) indicates that this species can be expected to survive better in fine than in coarse soils.

Part of the reason for the adaptability of sweetgum is the plasticity of its root form. The root system varies from very shallow with no taproot in swamp situations, to a very deep taproot on dry hillsides (Chittenden, 1906; Trenk, 1929; Thomas, 1961).

Roberds (1965), in a study of variation in sweetgum seedlings from several areas throughout North Carolina, found differences between sources in corkiness of the bark, which could be correlated with the May-August precipitation of the source area, and in time of leaf abscission, correlated with the annual temperature, frost free season, and longitude of the source. This suggests the existence of physiological races in the species within this state. Physiologically distinct ecotypes, which may or may not be morphologically distinct, may exist within a given species, and may occupy edaphically or climatically different areas (Clausen and Heisey, 1958). It was thought that such a situation might exist within a single geographic population of sweetgum which occupied both wet, bottomland sites and drier upland sites within the same locality.

Growth of sweetgum was found to be very sensitive to soil moisture (Ferrell, 1953), and water was more important than

light and nutrients in determining dry weight and height growth of one year old seedlings (Post, 1962). Any genetic differences between edaphic ecotypes of sweetgum, if such exist, would probably be reflected in their photosynthetic capacities, and specifically in the change in photosynthetic rate during drought, since available moisture is so important to the growth of sweetgum.

The effect of soil moisture on photosynthesis of tree seedlings has been investigated for several oaks (Bourdeau, 1954; Kozlowski, 1949), loblolly pine (Kozlowski, 1949), and pecan (Loustalot, 1945), and for small apple trees (Schneider and Childers, 1941). Bormann (1953) found that photosynthesis of sweetgum seedlings declined slowly at first, as soil moisture decreased, then rapidly, with net photosynthesis reaching zero just above the wilting point of the soil.

However, the physiological processes of a plant are affected directly by the energy status of water in the plant, which is dependent on the rate of water loss by the plant relative to the rate of absorption (Brix, 1962). Thus the response of a plant cannot be explained solely on the basis of soil or atmospheric conditions (Vaadia, Raney and Hagan, 1961). Unfortunately, few measurements of photosynthesis have been accompanied by measurement of the energy status of water in the plant. Post (1962) related photosynthetic rate to relative

turgidity, a somewhat better measure of plant water stress than soil moisture. Brix (1962) determined that increasing water stress, measured as the diffusion pressure deficit of the leaves, reduced photosynthesis of loblolly pine and tomato. Boyer (1965), using osmotically produced water stress, studied the reduction in photosynthesis and respiration in cotton.

The purpose of this study is to determine what differences, if any, exist in the photosynthetic and respiratory rates of an upland and a bottomland population of sweetgum seedlings, with high and low water stress. Water stress was measured by determining the water potential of the leaves with an electric psychrometer. It was decided to use seedlings established under natural conditions and transplanted, as they would have undergone some selection for the habitat they occupy. The seedlings would therefore be more likely to represent the type of genotype which mature trees in that area would have than would seedlings grown from seed in the greenhouse.

PHOTOSYNTHESIS AND RESPIRATION OF WELL-WATERED SEEDLINGS

Materials and Methods

Two groups of sweetgum seedlings were located on the Duke Forest near Durham, North Carolina, one (the "ridge" source) on a flat upland near the Animal Behavior Pens, the other (the "bottom" source) on the west bank of New Hope Creek. The latter was located just upstream from the bridge on Wooden Bridge Road and around the small parking area there. The topsoil of both areas was a sandy loam, the bottom area having 14% clay, and the ridge, 6.5%.

The bottom site was not as typical for such areas as one might want, being partially on a fairly steep bank. The ridge source was at the edge of a pine woods and was more typical of this type of site. The elevation of both areas was 360 ft. They were about seven miles apart.

About thirty seedlings, 20-50 cm. tall, were dug up at each area on Oct. 24, 1964. They were kept at 38°F. with their

roots in wet peat moss until Oct. 30, when they were planted in a 2:1:1 mixture of soil:sand:peat in 7 in. plastic pots. The seedlings were kept outside until Dec. 26, 1964, when they were moved into the greenhouse, where they remained throughout the experiment. The photoperiod was extended to 19 hours with incandescent lighting in order to break dormancy (Kramer, 1936). The bottomland trees ("B source") broke dormancy in 19-38 days (avg. 24.5 days) and the ridgetop trees ("R source") in 23-34 days (avg. 25.8). Some trees had been killed by the transplanting. The growing tips on a few others turned brown and died back, but when these were cut off and the cut surfaces treated with a fungicide, the dieback stopped. These seedlings developed normally afterwards, with a lateral bud taking the place of the terminal.

Thirteen healthy, well-formed seedlings were selected from each group for use in photosynthesis measurements. The R seedlings used were slightly larger in all dimensions and had slightly better root systems on the average than the B seedlings, but in no case were these differences significant. Ages of the seedlings ranged from 1 to 4 years, the average being 2.0 years for the ridge source and 2.2 years for the bottomland. The twenty-six seedlings were ordered randomly for each series of photosynthesis measurements. Each seedling was used once in each series.

The apparatus used to measure photosynthesis and respiration was similar to that described by Brix (1962), except that an "open" air-flow system was used. Air drawn from outside at a height of 60 ft. above the ground was pumped through an aquarium aerator in a water bath kept at 21 to 22°C. This presumably saturated the air and should have maintained a relative humidity about 56% in air at the temperature of the assimilation chamber (29 to 32°C). Air flow rate through the chamber was maintained at maximum pump capacity, which varied from 4.9 to 5.4 liters/min. Thus the air in the chamber was completely replaced about once every 15 min. A fan was operated in the chamber to insure thorough mixing of the air. Light intensity was 5000 to 6000 ft.-candles at the center of the chamber, and somewhat less toward the outer walls. Bormann (1953) found that photosynthesis in sweetgum reached light saturation between 1450 and 2900 ft.-candles. The light intensity on a horizontal surface exceeded this in all parts of the chamber.

The temperature control system, activated by a thermometer and a "Thermocap" relay, controlled a water pump. During photosynthesis measurements, cool water was pumped through the copper coils around the inner wall of the chamber whenever the temperature exceeded the desired limit. Warm water was used to maintain temperature during the respiration measurements. Because of the arrangement of the cooling

system air temperature during the photosynthesis measurements varied on a 6-7 min. cycle, from 29 to 32°C, the average over the cycle being 31.7. Respiration temperatures varied from 31 to 32°C over an 11 min. cycle, the average being 31.5. The temperature of the leaf tissue during the photosynthesis runs probably was somewhat higher than the air temperature (Gaastra, 1959), which meant the respiration and photosynthesis measurements were not made under strictly comparable conditions. However, the fan probably kept this temperature difference to a minimum.

These temperature and humidity ranges were chosen to represent the middle of an average summer day in the locality where the seedlings were obtained (U.S. Dept. Commerce, 1963). Humidity in the chamber varied considerably, depending on the rate of transpiration of the seedlings. However, Mitchell (1936) showed that the rate of carbon fixation in several garden plants is not affected by changes in atmospheric humidity within a fairly wide range.

All measurements of photosynthesis and respiration were made between 8 a.m. and 5 p.m. The plants were watered immediately before use, then placed with their stem in the chamber, reaching as close to the top as possible. The stem was sealed into the hole in the lower plexiglass cover of the chamber with modeling clay. A 90 min. equilibration period was

used. After calibrating the infra-red gas analyzer with gases of known carbon dioxide content, photosynthesis measurements were made. The CO_2 content of air from the supply line and from the chamber were measured alternately. The air flow rate into the chamber was recorded during each measurement. If changes occurred between measurements, they were repeated until equivalent values were obtained consecutively. Then the lights were shut off and the chamber was covered with a black cloth. After a 45 min. equilibration period, respiration was measured and the plant was removed from the chamber.

Leaf area was determined for each plant either just before or just after it was used. A transparent sheet of plastic with a grid of 1 cm. squares, with a dot in each quarter, was used to estimate leaf area. The number of full squares and dots covered by each leaf was recorded for each plant.

Two replications were made with the well-watered plants. The first was run 60 to 80 days after bud break, the second from 80 to 100 days. All plants produced new leaves throughout the period.

Results and Discussion

Rates of net photosynthesis and respiration were calculated as mg. of CO_2 absorbed or released per 100 cm.^{2} of

leaf area (one surface). The results are shown in Table 1, pp. 12 and 13. The rate of photosynthesis per unit of leaf area decreased as leaf area increased (Fig. 1 and 2, pp. 15 and 17) but respiration showed no such relationship. The probable reasons for this drop in rate of photosynthesis are the following:

1. As the leaf area increases a larger proportion is shaded than before, reducing the overall efficiency of the photosynthetic surface (Kramer, 1958).

2. Larger trees deplete the CO_2 in the air to a greater extent than smaller ones. In some cases, the air drawn out of the chamber had less than 60% of the CO_2 concentration of that entering. Since the air was well mixed by the fan, this means that the plant was operating at a CO_2 level which would limit its photosynthetic rate (Brix, 1962; Gaastra, 1959).

3. As the leaves aged their photosynthetic efficiency probably declined, as was shown for oak and maple by Richardson (1957).

The photosynthetic rates for well-watered plants are similar to those found by Post (1962) for non-fertilized one year old sweetgum seedlings, within the range of leaf areas common to the two experiments. This suggests that the results were not affected significantly by seedling size until leaf area exceeded about 700 $cm.^2$. Average respiration rates fell about half way between those found for pine and for eastern red oak by Kramer and Decker (1944).

TABLE 1

LEAF AREA, PHOTOSYNTHESIS AND RESPIRATION OF WELL-WATERED SEEDLINGS

		Replication 1			Replication 2		
Source	Seedling No.	Leaf Area in sq. cm.	Photosynthesis (Mg. CO_2/dm^2/hr)	Respiration	Leaf Area in sq. cm.	Photosynthesis (Mg. CO_2/dm^2/hr)	Respiration
Bottom	8	1136	5.25	1.00	1609	4.03	.93
	9	694	5.53	.95	1056	5.02	1.32
	12	412	5.31	.89	823	6.06	1.35
	13	236	4.61	1.29	376	5.92	1.33
	14	959	5.93	1.00	1004	6.07	.80
	15	655	7.59	1.24	779	6.90	.96
	20	484	10.13	1.87	484	9.39	1.42
	25	317	7.14	1.16	534	6.14	1.14
	26	1388	4.49	.84	1492	4.75	.50
	27	1340	3.93	.85	1650	4.29	.60
	28	634	7.87	1.15	756	6.71	1.03
	29	1234	5.25	.95	1593	4.75	.94
	30	977	4.48	.71	1258	5.15	.99
	Avg.	805	5.96	1.07	1032	5.78	1.02
Ridge	5	802	5.73	1.21	1410	5.01	.95
	6	725	4.31	.79	1091	5.13	.89
	7	930	5.55	1.12	1590	4.03	.96
	10	1128	4.23	.74	1519	4.13	.88
	16	1037	4.95	1.23	1585	4.49	.91
	17	1406	4.19	.87	1777	4.44	.96
	18	626	7.83	.80	762	6.55	1.31

TABLE 1 (CONTINUED)

Source	Seedling No.	Replication 1 Leaf Area in sq. cm.	Replication 1 Photosynthesis (Mg. $CO_2/dm^2/hr$)	Replication 1 Respiration (Mg. $CO_2/dm^2/hr$)	Replication 2 Leaf Area in sq. cm.	Replication 2 Photosynthesis (Mg. $CO_2/dm^2/hr$)	Replication 2 Respiration (Mg. $CO_2/dm^2/hr$)
	19	1031	5.75	1.22	1343	5.28	1.22
	20	1222	5.70	1.19	1287	5.33	1.02
	22	1022	4.77	.80	1372	4.65	.89
	23	533	7.65	1.59	885	5.02	.88
	28	243	12.71	.84	491	6.75	1.24
	29	976	5.56	.97	1412	4.15	.78
	Avg.	899	6.07	1.03	1271	5.00	1.00

Figure 1

Photosynthesis per Unit of Leaf Area over Leaf Area per Seedling. Well-watered Seedlings: Replication 1

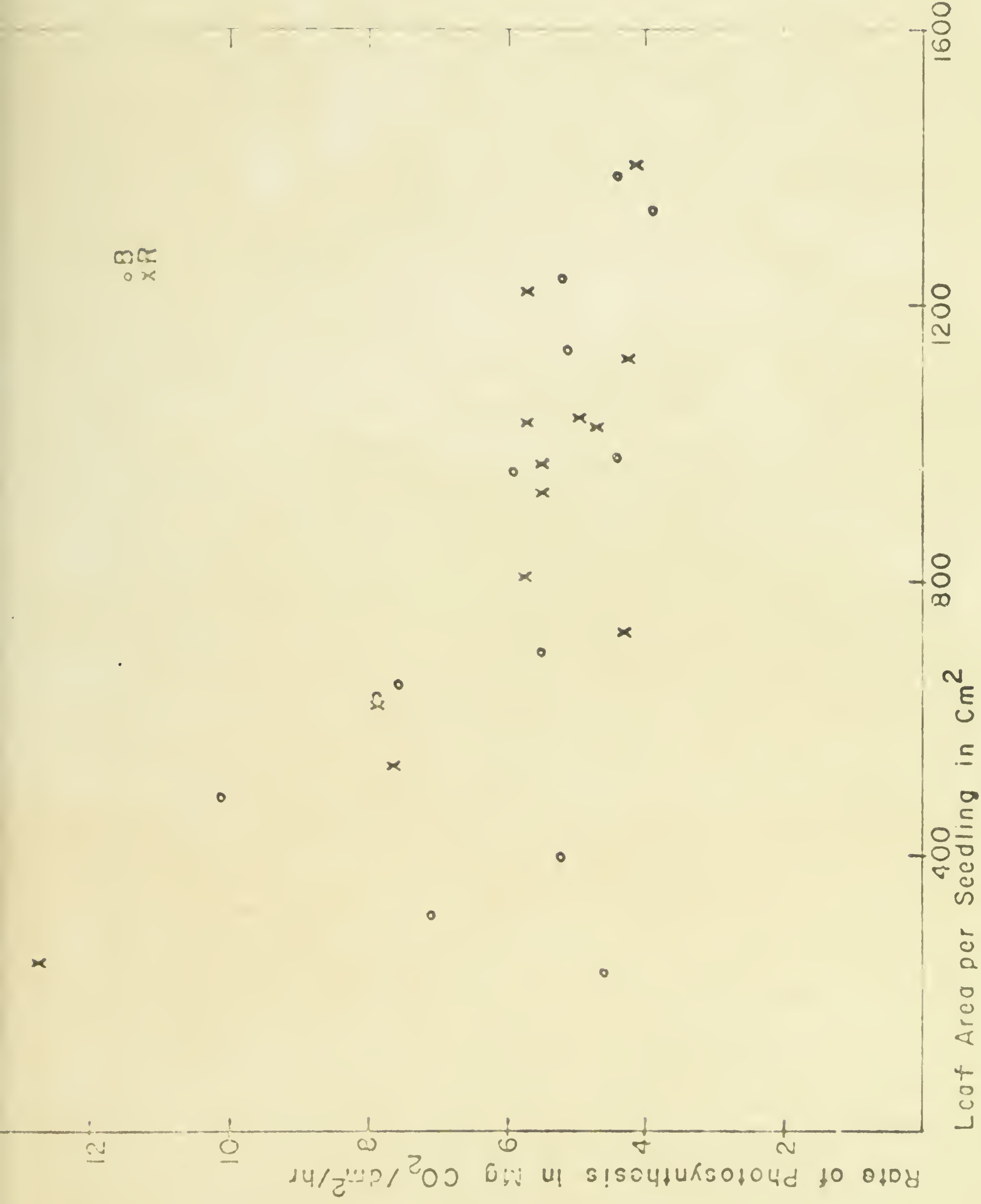
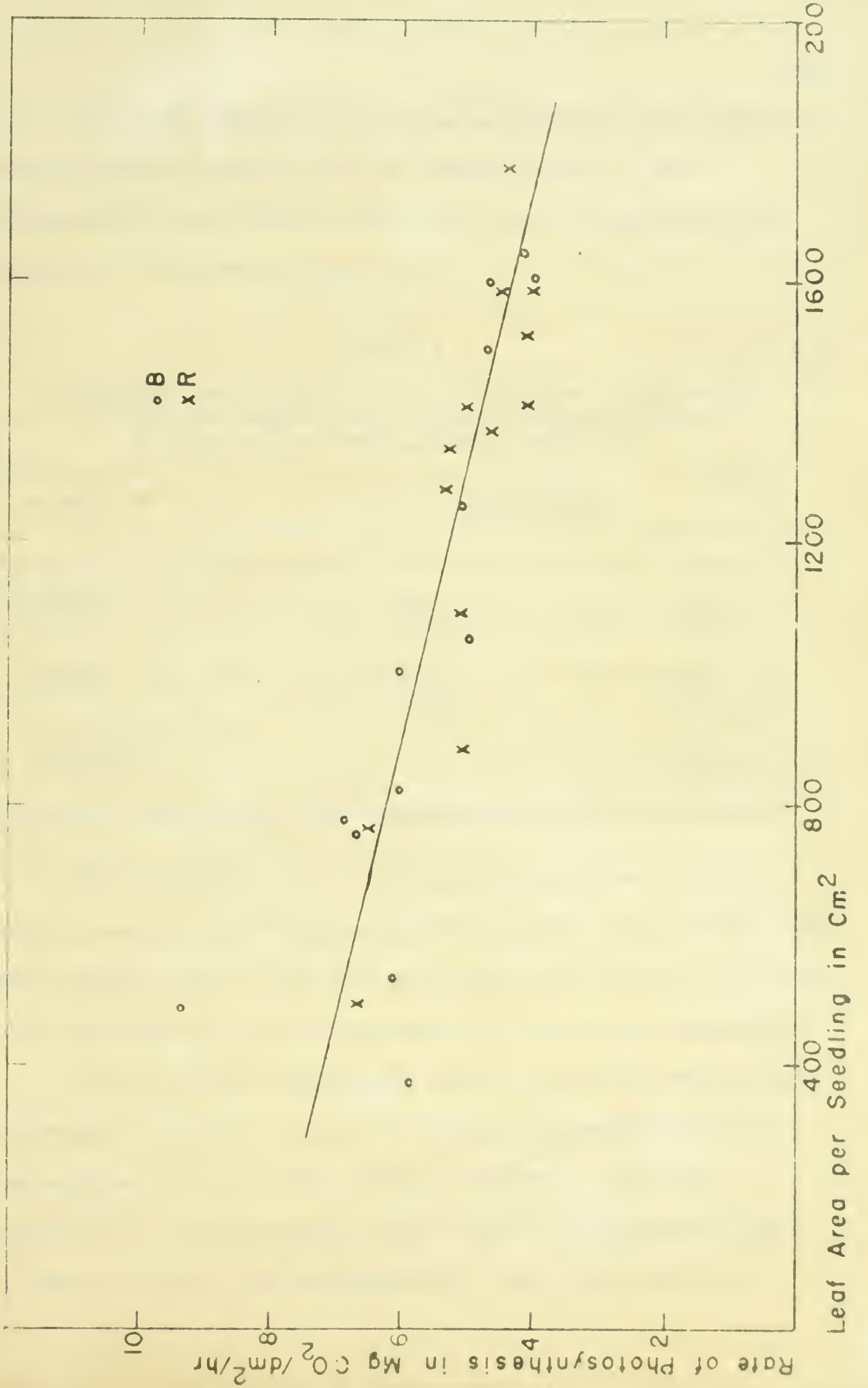

○ B
× R
12
10
8
6
4
2
400
800
1200
1600
Leaf Area per Seedling in Cm^2
Rate of Photosynthesis in Mg CO_2/dm^2/hr

Figure 2

Photosynthesis per Unit of Leaf Area over Leaf Area per Seedling. Well-watered Seedlings: Replication 2


o B
x R
Rate of Photosynthesis in Mg CO2 /dm2/hr
10
8
6
4
2
Leaf Area per Seedling in Cm2
400
800
1200
1600
2000

The relationship of leaf area to photosynthetic rate is shown for the two replications in Figures 1 and 2. The regression and correlation coefficients for the rate-leaf area regressions are given in Table 2.

TABLE 2

CORRELATION COEFFICIENTS (r) AND REGRESSION COEFFICIENTS (b) FOR THE REGRESSION OF RATE OF PHOTOSYNTHESIS ON LEAF AREA FOR WELL-WATERED SEEDLINGS

Source	Replication	
	1	2
Bottom	r = -.501 b = -.00224	r = -.784 b = -.00244
Ridge	r = -.816 b = -.00607	r = -.869 b = -.00202
Combined		r = -.823 b = -.00236

The first replication of the R source shows a significantly greater drop with increasing leaf area than do the other three groups. This is due in large part to one plant, R28, which had a very high rate of photosynthesis in the first replication.

In the second replication, there is no difference in the performance of the two sources. Both fall on essentially the same regression line. This combined regression line for replication 2, extrapolated in some cases to larger leaf areas, was used to predict the photosynthetic rates which would be

expected with no water stress when the plants were later subjected to water stress.

Average respiration values showed no statistically significant differences between replications or between sources, although the average rates decreased slightly from the first to the second replication for both sources. They varied considerably from tree to tree within sources and between replications for the same tree.

There seem to be no well-defined differences in respiration and photosynthesis of well-watered trees between the ridge and bottom sources. The only suggestion of a difference is the different regression coefficient for the R seedlings in the first replication. It may be that the increasing limitation of the CO_2 concentration as the trees grew caused any differences which might have shown up with smaller trees or better air supply to disappear.

REACTION OF PHOTOSYNTHESIS AND RESPIRATION TO WATER STRESS

Materials and Methods

The same seedlings and equipment were used as before. The experiment was run 105 to 125 days after initial bud break. Most plants had set a terminal bud by the end of the period. Plants were not watered for several days before measurements of photosynthesis were made. Immediately after the respiration measurements, water potentials were determined on the fourth or fifth leaf from the stem apex, using a thermocouple psychrometer (Richards and Ogata, 1958; Boyer, 1965). About half the measurements were made with a double thermocouple arrangement, allowing correction for respiration heat of the leaf tissue (Barrs, 1965; J.S. Boyer and E.B. Knipling, personal communication, 1965). The rest of the readings were corrected for respiration heat using an average correction figure from the double thermocouple. An average correction factor of 1.07 was then applied to all water potentials to compensate for errors due to leaf resistance which cause the readings to indicate a higher

water potential than exists (J.S. Boyer and E.B. Knipling, personal communication, 1965). The tissue was very slow to equilibrate, taking 6 to 10 hours. The energy status of the water in the leaves was expressed as the "water potential", in terms of bars (1 bar = 0.987 atm), as discussed by Boyer (1965).

Water potential measurements made on seedlings not used in the photosynthesis experiments showed that there tends to be a difference of 0.5 to 2.0 bars between an upper, middle and lower leaf on average-sized seedlings. Potentials in the top leaves of well-watered seedlings (which had average water potentials of -3.5 to -6.0 bars) were as high or slightly higher than the lower ones. This could be expected since young leaves seem to obtain water at the expense of the older ones (Kramer and Kozlowski, 1960; Vaadia et al., 1961). However, in the dryer trees there was no detectable pattern. It seems that the fourth leaf gave a good representation of the water stress of the plant.

The seedlings were divided into three "stress groups" for analysis of the data. Those with water potentials above -8 bars were considered to have low water stress. Water potentials of -8 to -11 bars were considered to constitute moderate stress. Those seedlings with water potentials of less than -11 bars had high water stress. These stress groups seem to have a biological basis rather than being completely arbitrary. For example, the

-8 bar limit for the low stress group corresponded to the lowest water potentials found in "well-watered" plants and to the limit used by Brix (1962). He found that photosynthesis of loblolly pine ceases at a diffusion pressure deficit of 11 atm. (approximately equal to a water potential of -11 bars). Sweetgum reacted about the same way.

Photosynthesis and respiration were determined as before. An "expected" photosynthetic rate for each tree was calculated using the rate-leaf area regression determined in replication 2. The deviation of each tree from its expected value, expressed as a percent of the expected value, was determined and used for statistical analysis of the data. Use of actual deviations in the analysis could lead to incorrect conclusions, because average leaf areas of the stress groups (and therefore their expected photosynthetic rates) were considerably different in some cases.

A porometer (Shimshi, 1963) was used to examine stomatal behavior. Relative stomatal aperture was measured by recording the time it took the pressure to fall from 180 to 160 mm.

Results

Photosynthesis and respiration rates for the various seedlings, with their corresponding water potentials, are shown in Table 3, p. 23. The percentage reduction of photosynthesis

TABLE 3

RATES OF PHOTOSYNTHESIS AND RESPIRATION WITH VARYING WATER STRESS

Source	Seedling No.	Leaf Area in sq. cm.	Photosynthesis	Respiration	Water Potential in bars
			(Mg. $CO_2/dm^2/hr$)		
Bottom	8	2066	.25	.83	-10.7
	9	1429	.27	.57	-12.4
	12	1535	.38	.98	-10.0
	13	599	2.85	1.02	- 8.2
	14	1225	5.33	.81	- 7.2
	15	1246	4.80	.90	- 4.3
	20	1115	.00	1.08	-15.1
	25	590	5.38	.39	- 5.7
	26	1574	3.94	.49	- 8.8
	27	1720	- .07	.66	-16.4
	28	1106	2.63	.66	- 7.7
	29	1821	.41	.72	- 9.4
	30	1543	2.31	.45	-10.5
	Avg.	1352		.74	- 9.7
Ridge	5	1794	.68	.74	-10.9
	6	1800	2.36	.54	- 4.5
	7	1954	- .06	.93	-11.5
	10	1910	1.57	.55	- 9.6
	16	1858	1.92	.75	- 8.9
	17	2387	1.89	.96	- 8.2
	18	963	1.33	.69	- 9.4
	19	1620	2.45	.93	- 7.6
	20	1927	.06	.83	-15.8
	22	1725	.61	.74	-11.4
	23	1207	4.68	.80	- 8.8
	28	500	7.25	.89	- 4.6
	29	1578	3.87	.72	- 3.8
	Avg.	1633		.78	- 8.8

is plotted over water stress in Figure 3, p. 26. Average reductions in photosynthesis from expected values for the various stress groups and the two sources are shown in Table 4.

TABLE 4

AVERAGE PERCENTAGE REDUCTION IN PHOTOSYNTHETIC RATE

Water Stress Group	No. Trees per Source	Source		
		Bottom	Ridge	Combined
Low	4	19.25	22.25	20.75
Moderate	6	64.67	49.50	57.09
High	3	98.67	95.00	96.84
Average	13	58.54	51.62	

The analysis of variance of the percentage reduction of photosynthetic rates by water stress is shown in Table 5.

TABLE 5

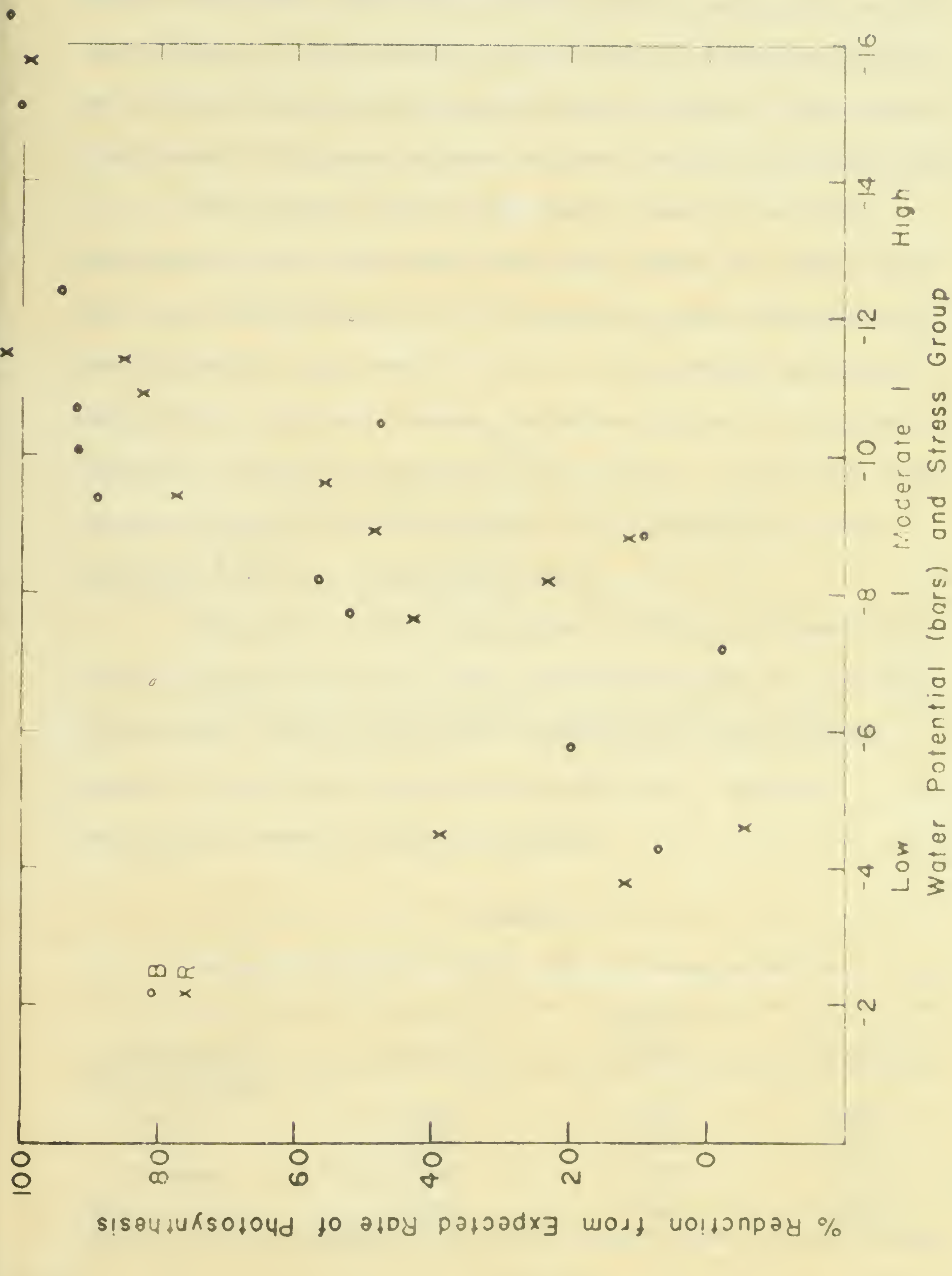
ANALYSIS OF VARIANCE OF PERCENTAGE REDUCTION IN PHOTOSYNTHESIS

Source	df	Sum of squares	Mean square	F-value
Treatment	5	20664.8	4133.0	6.418++
Source	1	311.5	311.5	NS
Stress	2	19936.6	9968.3	15.479++
Interaction	2	416.7	208.4	NS
Error	20	12879.1	644.0	
Total	25	33543.9		

NS = not significant
++ = significant at .01 level

Figure 3

Percentage Reduction in Photosynthesis by Water Stress


% Reduction from Expected Rate of Photosynthesis
100
80
60
40
20
0
-2
-4
-6
-8
-10
-12
-14
-16
Low
Moderate
High
Water Potential (bars) and Stress Group
o B
x R

There were highly significant differences in reductions between the different stress groups, but none due to different sources or to the interaction of source and water stress. There were no significant differences between sources for any one stress group.

The division into stress groups seems to be valid. Reductions in the low stress group vary widely but remain below 50%, with one exception. In the moderate group, reductions in photosynthesis vary from 10 to 92%. This probably indicates a wide genetic variation between individual plants of the photosynthetic response to moderate water stress. In the high stress group, all rates of photosynthesis are very low and in some instances below the compensation point.

There was a highly significant difference between the average respiration rates during the well-watered run and those during water stress conditions, although none exist between sources during either control or stress runs. Average respiration rates are shown in Table 6.

TABLE 6

AVERAGE RESPIRATION RATES (Mg CO_2 released/dm^2/hr)

Experiment	Bottom	Source Ridge	Combined
Well-watered			
Rep 1	1.069	1.034	1.052
Rep 2	1.023	0.999	1.012
Average	1.047	1.017	1.032
Water Stress	0.735	0.775	0.755

Although there seem to be no differences in the physiological processes of the two populations examined during this investigation, there are indirect evidences of differences. Average growth rates for height and leaf area, during the period from the first to the last experiments, are shown in Table 7. Although height growth was the same throughout the period for both populations, the ridge trees added leaves at a significantly faster rate.

TABLE 7

GROWTH RATES IN HEIGHT AND LEAF AREA

Source	Height (cm./wk.)	Leaf Area (cm.^{2}/wk.)
Bottom	1.50	79.8
Ridge	1.47	107.5

Discussion

The fact that the rate of photosynthesis decreases as available soil moisture declines is well documented. The pattern of this decrease in photosynthesis is not the same in all plants. Bormann (1953) showed that photosynthesis of sweetgum decreases slowly at first as soil water decreased, and more rapidly as the wilting point was approached. A similar situation was encountered with pecan (Loustalot, 1945), loblolly pine and oak (Kozlowski,

1949) and clover (Upchurch et al., 1955). However, the decrease in photosynthesis of small apple trees was faster during the middle of the drying period than at the end, when soil water was presumably at a minimum (Schneider and Childers, 1941). The lowest rates of photosynthesis found with the apple trees were well above the compensation point, while pine, oak and sweetgum reached compensation point around the wilting point of the soil.

Post (1962) compared the reduction of photosynthesis in yellow poplar with that in relative turgidity of the leaves as well as with the decrease in soil moisture. He found that the rate of photosynthesis decreased slightly faster as soil moisture continued to decrease, but that it was linearly related to the relative turgidity of the leaves. Brix (1962) found that photosynthesis of loblolly pine and tomato was unaffected until the diffusion pressure deficit of the foliage reached 4 atm. in pine and 7 atm. in tomato. At higher deficits (i.e. lower water potentials) the rate of photosynthesis decreased linearly as the deficit increased, reaching essentially zero at deficits of 11 and 14 atm., for pine and tomato respectively. Boyer (1965) found a linear decrease in photosynthetic rate per unit of leaf area in cotton, as the water potential decreased.

The present results show a pattern similar to those of Brix (1962), with a decrease in photosynthesis as the water potential decreases until photosynthesis essentially stops when a

water potential of -11 bars is reached. This decrease occurs in an approximately linear fashion.

The cause of this reduction in photosynthesis by increasing water stress has not been completely defined. A major part of it is thought to be due to an increase in resistance in the CO_2 pathway from the air to the chloroplasts. This is probably controlled by the stomata under conditions of high light, but in other situations considerable closure of stomates may occur without affecting photosynthesis (Gaastra, 1959). Appreciable rates of photosynthesis have been observed when microscopically examined stomata appeared to be closed (Mitchell, 1936; Schneider and Childers, 1941). There is evidence that an important resistance to diffusion of CO_2 may also develop at the surfaces of the mesophyll cells as the water potential of the leaves decreases (Gaastra, 1959; Shimshi, 1963). It is also thought that water stress affects the hydration of enzymes, which may change their activity. This could change the rates of photosynthesis and respiration (Vaadia *et al*., 1961; Boyer, 1965).

A third mechanism for the effect of water stress on photosynthesis is the decreased permeability which Brix (1962) found it caused in roots of loblolly pine. This change delayed the recovery of photosynthesis after a wilted plant was rewatered compared to a plant from which the roots were removed.

In the present study, no effort was made to determine the cause of the reduction in photosynthesis and respiration by water stress. However, a few measurements of stomatal resistance were made with a porometer. These indicated that the stomata remain open in very low light intensities. No increase in resistance was found in leaves with water potentials as low as -8 bars. Potentials of -16 bars, which caused wilting of the leaves, were associated with large increases in stomatal resistance. Porometer readings on these seedlings were difficult to replicate, varying between leaves and within a given leaf. This made small variations in stomatal resistance difficult to distinguish.

The effect of water deficits on dark respiration in plants is not so well known as that on photosynthesis. In apple trees respiration increased, reaching rates up to 160% of its initial value, while photosynthesis decreased with decreasing soil moisture (Schneider and Childers, 1941). Upchurch and his co-workers (1955) found respiration to increase slightly in clover at a soil moisture content just above that at which photosynthesis began to decline. On the other hand, Brix (1962) found respiration in tomato to be reduced by water stress, while it varied in loblolly pine depending on the severity of the stress. He suggested that the initial decrease in pine at diffusion pressure deficits of less than 16 atm. was due to

less photosynthetic substrate being available. Respiration then increased up to a DPD about 36 atm. because increased hydrolysis of starch increased the amount of substrate available. Respiration decreased rapidly at higher DPD's. Boyer (1965) found a decrease in respiration rate of cotton as water potential of the plant growth medium decreased. The magnitude of the decrease in respiration found in his experiments and of the initial decrease in pine found by Brix was about the same as occurred in the present experiments.

Respiration rates during the water stress experiments showed no defineable relationship to the magnitude of water stress. This could be expected because of the large differences between individuals during the control runs. A definite pattern might have shown up had each seedling been measured at several levels of water stress. However, there was a significant reduction in average rates of respiration from the control experiments to those with water stress. Respiration has been shown to be somewhat higher in newly expanded leaves of oak and maple than in older ones (Richardson, 1957). If similar situations exist in sweetgum, it may have contributed to the reduction of respiration in the somewhat older leaves present at the time of the water stress experiments. The reduction from the second replication with well-watered plants to the water stress run was of a much greater magnitude than that which

occurred between the first and second replications, although the increases in age were equivalent. Therefore it seems that most of the reduction of respiration was a result of the reduced water potential of the plants.

The differences which might be expected to exist between the two sources of sweetgum seedlings were not found with the methods and material used. More differences might be found if the factor of limiting CO_2 concentration in the assimilation chamber were removed. Although there are some indications of physiological differences between the populations, there is little definite evidence of major differences in the reaction of photosynthesis and respiration to water stress. The separation of the two habitats used from one another, by either ecological conditions or by distance, is probably not sufficient for distinct physiological races to develop. Gene exchange between mature sweetgum in contrasting habitats probably occurs, since sweetgum is wind-pollinated and largely self-sterile. This would probably maintain a very plastic and highly variable species (Schmitt and Perry, 1964). The development of distinct physiological ecotypes is probably not necessary for the species to maintain itself in the contrasting habitats which it occupies. It appears that the physiological races of sweetgum proposed earlier in this paper may not have developed within the limited geographical area from which these seedlings were obtained.

SUMMARY

Measurements were made of the rates of photosynthesis and respiration of sweetgum seedlings taken from an upland and a bottomland habitat on the Duke Forest. Comparisons of the rates for well-watered conditions were made with those during water stress, which was defined by the water potential of the leaves. Water stress significantly reduced respiration and photosynthesis in both seedling populations. Differences between the populations were too slight to support the hypothesis that distinct physiological races of sweetgum have developed in these ecologically different habitats.

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